Neurobiology of Learning and Memory 119 (2015) 85–92

Contents lists available at ScienceDirect

Neurobiology of Learning and Memory

journal homepage: www.elsevier.com/locate/ynlme

Variable motor imagery training induces sleep memory consolidation and transfer improvements

Ursula Debarnot [a,b,c,*], Kouloud Abichou [a,b], Sandrine Kalenzaga [a,b,d], Marco Sperduti [a,b], Pascale Piolino [a,b,e]

[a] Centre de Psychiatrie et Neurosciences (Inserm UMR S894), Université Paris Descartes, Paris, France
[b] Laboratoire Mémoire et Cognition, Institut de Psychologie, Boulogne Billancourt, France
[c] Département des Neurosciences Fondamentales, CMU, Université de Genève, Michel-Servet 1, 1211 Genève, Switzerland
[d] Centre de Recherches sur la Cognition et l'Apprentissage (UMR-CNRS 7295), Université de Poitiers, France
[e] Institut Universitaire de France, Paris, France

ARTICLE INFO

Article history:
Received 26 February 2014
Revised 11 December 2014
Accepted 23 December 2014
Available online 3 January 2015

Keywords:
Motor imagery
Practice structure
Acquisition
Consolidation
Transfer
Contextual interference

ABSTRACT

Motor-skill practice in repetitive or variable orders leads to better within-day acquisition and facilitates retention and transfer, respectively. This practice pattern effect has been robustly found for physical practice, but little is known about its effect after motor imagery (MI) practice. In the present study, we investigated the effect of constant or variable MI practice, and the consolidation following a day-time or a sleep interval. The physical performance was assessed before (pre-test) and after MI training (post-test), as well as after a night or day-time consolidation (retention test). Finally, a transfer test on an unpracticed task was further performed. Results revealed that in all participants, performance increased significantly in the post-test when compared with the pre-test, while only subjects in the variable MI training showed further gains in performance in the retention test following a night of sleep, and exhibited the best transfer of performance to a novel visuomotor sequence. In contrast, subjects in the constant MI training did not show any delayed performance gain following both day and sleep-consolidation. Overall, and for the first time, these findings partially support the practice pattern effect of motor learning with MI, and further highlight a new difference between mental and physical practice, especially on consolidation. To conclude, variable MI practice, rather than constant, seems to be the valuable condition that should be considered in the practical implications of mental training in motor learning and rehabilitation.

1. Introduction

A wide range of experimental studies have provided strong evidence that training conditions that make the performance harder during practice improve long-term retention (Schmidt & Bjork, 1992). Especially, previous works have shown that when only one motor skill is learned in a single session, its acquisition is facilitated compared to when multiple skills are learned, while such latter condition of practice leads to a better retention and transfer. This acquisition–retention 'paradox' is termed the contextual interference effect (CI, Battig & Shea, 1980) and is well-documented in the motor learning literature (Brady, 2008 for review).

Classically, motor training structure can be positioned on a continuum between a simple structure such as constant practice, and more complex structures, such as variable practice. A constant practice structure consists in performing the same task in a row, whereas variable practice structure consists in the execution of a motor task randomly interleaved with trials of different motor tasks. Interestingly, it has been demonstrated that variable practice, rather than constant, results in a stronger and more flexible representation of the movement (Albaret & Thon, 1998). Two theoretical positions have emerged to explain the CI effect. On the one hand, some authors suggest that when practice is undertaken in a variable order, the learning benefit occurs by the introduction of two or more similar tasks into working memory (Shea & Morgan, 1979). The interference created in working memory during practice results in an enhanced elaborative and distinctive processing that ultimately facilitates retention. On the other hand, interference might lead to forget action plans in working memory, thus necessitating the reconstruction of plans on each new trial under variable conditions (Lee & Magill, 1983). Such reconstruction process is suggested to facilitate the retention of the practiced skill

* Corresponding author at: Département des Neurosciences Fondamentales, CMU, Université de Genève, Michel-Servet 1, 1211 Genève, Switzerland. Fax: +41 22 37 95 402.

E-mail address: Ursula.debarnot@gmail.com (U. Debarnot).

http://dx.doi.org/10.1016/j.nlm.2014.12.010
1074-7427/

and the ability to generalize the existing knowledge from the practiced skill to a new situation, or in other terms the transfer of performance. Recently, Kantak, Sullivan, Fisher, Knowlton, and Winstein (2010) hypothesized that differences in the practice structure may drive subsequent offline activity in distinct neural structures that are critical to motor-memory consolidation. Using repetitive transcranial magnetic stimulation (rTMS), they demonstrated that transient inhibition of the dorsolateral-prefrontal cortex (DLPFC), but not of the primary motor cortex (M1), 24 h after variable practice, attenuated motor-skill retention, whereas the reverse effect was reported after constant practice. Therefore, motor memory consolidation engages distinct neural substrates that depend on the practice structure. In a subsequent study, the same authors extended the dissociation between the DLPFC and M1 processing with respect to variable and constant practice to the transfer of the learned skill (Kantak, Sullivan, Fisher, Knowlton, & Winstein, 2011). Taken together, these findings suggest that M1 contributes to motor memory consolidation and transfer following constant practice, while processing within the DLPFC is necessary when variable practice is at stake. It is likely that the benefits of variable practice to transfer to unpracticed movements, compared to constant practice, might be due to the development of a generalized 'schema' that is inferred or adapted from experience of different practice conditions (Shea & Kohl, 1990). Taking advantage of variable practice in motor skill consolidation and transfer, paradigms investigating schema notions to facilitate motor adaptation should be expanded.

In the wealth of the mental practice literature, motor imagery (MI) is a reliable complement to physical practice in enhancing cognitive and motor performance (Guillot & Collet, 2008), hence promoting the consolidation process toward the long term memory system (Jackson, Lafleur, Malouin, Richards, & Doyon, 2001). MI is the mental simulation of an overt action without any corresponding motor output, and substantially contributes in improving motor learning and performance (for reviews, see Driskell, Copper, & Moran, 1994; Feltz & Landers, 1983; Guillot & Collet, 2008). It is now well-established to what extent goal-directed actions, whether executed or imagined, share common neuro-cognitive processes. For instance, several experiments have provided evidence that there is a correlation between the duration of a mentally simulated action and that of the overt execution of the same movement (functional equivalence, Holmes & Collins, 2001). Moreover, executing or imagining an action recruits similar (albeit not identical) neural substrates (Decety, 1996; Lotze & Halsband, 2006). Up to now, only one study investigated the effect of practice structure using either physical or MI practice on motor skill learning, but only the acquisition phase was tested (Coelho, Nusbaum, Rosenbaum, & Fenn, 2012). Results showed that both physical and MI practice elicited significant improvement of performance in a post-training test, while variable practice was better than constant only when practiced physically. These data somewhat challenge the classical higher benefit in performance of constant compared to variable practice during physical acquisition. Additionally, the authors discussed the claim that motor representations for both overt and imagined movements are qualitatively equivalent. However, the effects of practice structure with MI during the retention and the transfer processes of motor learning have not been directly assessed thus far. Regarding the consolidation process, Debarnot et al. (Debarnot, Castellani, & Guillot, 2012; Debarnot, Castellani, Valenza, Sebastiani, & Guillot, 2011; Debarnot, Creveaux, Collet, Doyon, & Guillot, 2009; Debarnot et al., 2009) demonstrated sleep-related gains of performance on an explicit sequence of finger movements with MI, while using an observation learning of a sequential arm movement Trempe, Sabourin, Rohbanfard, and Proteau (2011) found a stabilization of the motor skill and its long-term retention. These contrasting insights in the consolidation process between MI and observation learning may relate to the difference in the nature of the motor task, but there is still a substantial lack of knowledge on this issue.

The present study thus aimed to investigate in which extent constant and variable structures of motor practice with MI might impact the performance in the acquisition, the consolidation and the transfer processes. First, we tested the effect of constant and variable MI training on a visuomotor sequential task during the acquisition session. Then, we explored whether the different structures of MI training (i.e., constant vs. variable) elicited different effects in performance following 10 h of consolidation (with or without intervening sleep) as well as on a transfer task. To address these issues, participants were randomly assigned to five different groups subjected either to constant or variable MI training, with half of them re-tested after a night of sleep and the other half after the same interval without sleep; a group that did not received any training was tested as a control group: MIC Night group, MIV Night group, MIC Day group, MIV Day group and no-training group. Motor performance was evaluated before the MI training, as well as just before and after a night- or day-time consolidation. Based on the CI effect as well as the functional equivalence between MI and physical practice, we predicted that compared to the no-training group, MI groups would demonstrate an improvement in performance following the training session, whereas the MIC group would show better performance than the MIV group after the acquisition session (i.e., post-training). By contrast, we hypothesized that greater offline delayed gains and better transfer of performance would be observed in the MIV group especially following a night of sleep, whereas those in the MIV day, MIC and no-training groups would not.

2. Method

2.1. Participants

A total of 71 healthy volunteers aged 18–40 years (mean age: 25.1 ± 6 years; 42 women) took part in this study. They were right handed, as assessed by the Edinburgh Handedness Inventory (Oldfield, 1971). None had any prior history of drug or alcohol abuse or neurologic, psychiatric, or sleep disorders, and they were instructed to be drug and alcohol free for 24 h prior to and during the experiment. Additionally, they reported sleeping regularly between 7 and 9 h per night, and extreme evening- and morning-type individuals, as well as regular nappers, were excluded based on subjective reports. This study was approved by the Ethics Committee of the University Paris Descartes, and all participants signed an informed consent.

2.2. Design and apparatus

Participants were tested in a quiet room, without any distracting stimuli, in order to help them focusing on the motor task. They seated on a chair at a distance of 35 cm from a keyboard and 45 cm in front of a 17-in. computer screen. A computer mouse was disposed 30 cm forward the keyboard (Fig. 1A). Such standardized distances between the subject and the experimental material (screen, keyboard and mouse) were suitable for a large range of individual. All participants were tested on a sequential finger task, consisting in moving the index finger of the left hand (nondominant) from the left button of the computer mouse toward 4 colored targets on the keyboard. The four keys A, F, I, M (AZERTY keyboard) were respectively colored in blue, red, green and yellow. All other keys were black but still functional; hence the sequential finger movements required precision to be correct. On each trial, four colored circles (3 cm in diameter), corresponding to the four key on

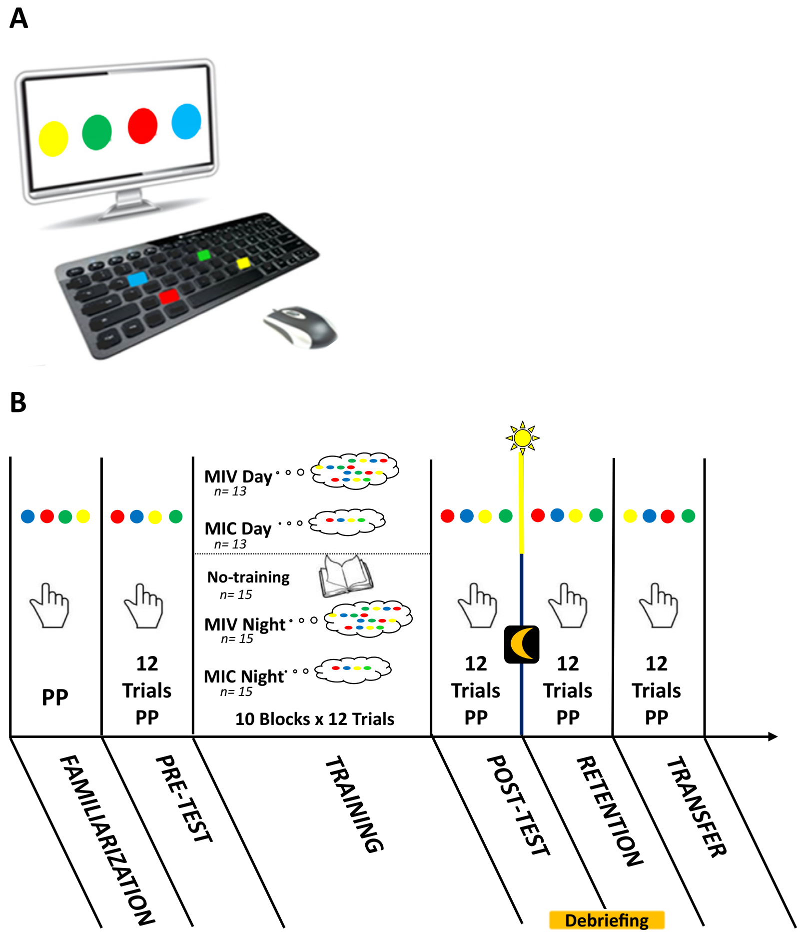

Fig. 1. Protocol of the experiment. (A) Illustrations of the setup and design of the MR Task. (B) Schematic view of the experimental protocol. All participants performed a pre-test session (baseline), which was followed either by a constant MI training (MIC groups) or variable MI training (MIV groups) or no-training condition (no-training group). Then, all participants performed a post-test session to assess the effect of MI training (or no-training) and they were re-tested following either a 10 h interval that included a night of sleep or a similar time interval without sleep during the daytime (retention test). Finally, a transfer test was performed.

the keyboard, appeared on a white screen. Subjects were requested to perform the sequence presented on the screen as fast and accurately as possible. Practically, four back and-forth movements, from the left button of the computer mouse toward the targets on the key-board, composed one trial; hence nine keys had to be pressed to produce a motor sequence. Each trial finished when subjects pressed the left button of the mouse (i.e., ninth movement) after reaching the last target on the keyboard. No feedback was provided to the subject about his/her performance, neither during the execution of sequential movement nor after the end of a block. To start a new trial the subjects had to press the space bar with the index finger of the right dominant hand. Stimuli presentation and data recording were automatically implemented using *PsychoPy* (Peirce, 2007).

2.3. Baseline measures

The revised Movement Imagery Questionnaire (MIQ-3, Williams et al., 2012) was administered to measure the individual's ability to form kinesthetic and visual mental images. The MIQ-3 is a 12-item self-report questionnaire, in which participants have to rate the difficulty of forming a mental representation using three 7-point scales referring to external visual imagery, internal visual imagery, and kinesthetic imagery. The Corsi Block Test (Milner, 1971) was also administered to estimate the individual visuospatial working memory capacity. In addition, the Wisconsin Card Sorting Test (WCST) was used to assess executive functioning (i.e., flexibility and perseveration, Heaton, Chelune, Talley, Kay, & Curtis, 1993). All participants were also asked to fill out the Pittsburg Sleep Quality Index (PSQI, Buysse, Reynolds, Monk, Berman, & Kupfer, 1989) to assess sleep quality and quantity. This test was administered to exclude participants who were experiencing obvious disturbances during their sleep–wake cycles and to ascertain the participants' predisposition to benefit from the natural effects of sleep on memory consolidation. Subjective measures of alertness and fatigue were also collected using the Stanford Sleepiness Score (SSS, Hoddes, Dement, & Zarcone, 1972). The SSS is a 7-point scale, with 1 being the most alert state. This questionnaire was presented before the familiarization and the retention sessions (see below).

2.4. Experimental procedure

The experiment was divided into six phases illustrated in Fig. 1(B).

(1) *Familiarization session:* The experiment was scheduled to begin at 8:00 pm in the Night groups and at 9:00 am in the Day groups. During this session, all subjects were asked to perform a few trials until they executed two consecutive

correct sequences. The familiarization sequence corresponded to the spatial disposition of the targets on the keyboard (i.e., from left to right: blue, red, green and yellow).

(2) *Pre-test:* It consisted in 12 trials of the same sequence of movement (red, blue, yellow, green), during which the subject had to execute physically the motor sequence, as fast and accurately as possible. This test block lasted about 2 min and was separated from the training session by a 1 min rest period during which the participants were asked to not imagine or to perform any sequential finger movements.

(3) *Training session:* Subjects from MI groups were asked to imagine the sequential finger task during 10 blocks of 12 trials each, separated by a resting period of 20 s. At the beginning of the experiment, a validated imagery script was read to the MI participants and briefly repeated right before the MI training, in order to ensure that they followed the instructions throughout MI sessions (see Appendix). Subjects from MI groups were asked to imagine themselves performing the motor sequence using a combination of visual and kinaesthetic imagery, i.e., imagining movement from within one's body and perceiving the sensations induced by executing the sequence. They were also asked to conform to the correct sequence and to imagine its execution at the same speed as during the pre-test session. The MIC groups (Night and Day) repeated the same finger sequence used during the pre-test session (red, blue, yellow, green), while the MIV groups (Night and Day) performed three new finger sequences (green, yellow, blue, red/yellow, blue, green, red/blue, green, red, yellow), as well as the test sequence. Three trials of each sequence were randomized within each training block. To prevent any actual finger movements, the participants were asked to leave their left hand motionless over the table, such as the experimenter could visually check whether the subject moved this hand during the mental rehearsal of the sequential movements. Participants were requested to keep their eyes open in order to see the stimuli sequences on the screen as well as rest periods between blocks. To be able to record the duration of each sequential movement, MI participants were asked to press the left button of computer mouse with the right index finger when they started the sequence mentally and to press it again to indicate the end of the sequential movement. As before, subjects pressed the space bar with their right index finger to generate another trial. During this session, subjects from the no-training group did not receive any MI training, instead, they were asked to read a magazine of their choice (Gentili, Papaxanthis, & Pozzo, 2006) during a period of time equivalent to that of the mental training (≈20 min). When required, the experimenter turned the pages of the magazine.

(4) *Post-test:* This session consisted of 12 physical trials of the test sequence, similar to the pre-test, performed by all subjects to evaluate their performance either after MI training or no-training. The procedure was exactly the same as that of the pre-test: participants were asked to physically execute the sequential finger task as fast and as accurately as possible. Finally, individual debriefings were performed for MI subjects to ensure that they fulfilled the MI instructions, and to determine whether they encountered difficulty in forming mental images. They were also asked to auto-evaluate the quality of their mental images using a Likert-type scale (from 1 = poor mental representation to 5 = vivid mental representation).

(5) *Consolidation:* The post-test was followed either by a night of sleep or an equivalent daytime period. All participants were clearly instructed not to perform any MI or physical practice of the sequential finger task between the post-test and retention sessions.

(6) *Retention test:* Finally, a retention test was administered either following an 8-h (±1 h) night of sleep (the session began 86 ± 25 min after waking up) or following a 10-h daytime period. Subjects of Night groups were first requested to answer to some questions about their night of sleep. For instance, they were asked about at what time they went to bed, whether they woke-up during the night, at what time they woke-up in the morning and the subjective sleep quality. Then, all subject performed a 12-trials session to evaluate the effect of day or sleep consolidation in motor performance. This retention session followed the same procedure as that used in the pre- and post-tests.

(7) *Transfer session:* After 2 min of rest, subjects were finally asked to perform a last 12-trials block. The finger sequence used in this session was new (yellow, blue, red, green). They were instructed to execute physically the sequential task following a different manner to perceive the sequence presented on the screen. Practically, when the four stimuli appeared on the screen, subjects had to identify the second stimuli as the first key to press, the fourth as the second, the first as the third and the third as the fourth. This new visuomotor association was chosen in order to maximize the probability to observe a transfer effect with respect to the practice pattern (constant or variable). Indeed, transfer tasks should be sufficiently different from the practiced task to provide evident effects (see Kantak et al., 2011 for details on this issue). Here, it remains that the transfer sequence had the same number of movements (i.e., four back and-forth movements) and timing/accuracy requirements were similar as during the acquisition session (pre-test, MI training, post-test). Thus, the transfer test provided an assessment of the ability to achieve a new goal using what was learned and consolidated before, i.e., abstract knowledge between the goal and action parameters to perform the sequential pointing task. Practically, the motor procedure was exactly the same as during the previous test sessions: the participants were asked to physically execute the sequential finger task with the left index finger as fast and as accurately as possible.

2.5. Data analysis

For each practice session (pre-test, post-test and retention), we analyzed two dependent variables, namely the mean number of errors and the mean sequence duration. To determine whether the initial performance was different between all groups, we performed a one-way analysis of variance (ANOVA) on the two dependent variables gathered in the pre-test. To investigate training and consolidation effects, we performed a repeated measures ANOVA on each dependent variable, with GROUP (MIV Day, MIC Day, no-training, MIV Night, MIC Night) as between-subjects factor and SESSION (pre-test, post-test and retention) as within-subjects factor. Imagined times were also considered to check whether the participants complied with the imagery guidelines; to do so, we used an $ANOVA_{RM}$ with GROUP (MIV Day, MIC Day, MIV Night, MIC Night) as between-subjects factor and SESSION (pre-test and MI training) as within-subjects factor. When appropriate, Tukey post-hoc comparisons were performed. To examine the effect of the type of training and consolidation process on the transfer of performance, we performed an $ANOVA_{RM}$ to compare the mean number of errors and the mean sequence duration between the pre-test and transfer sessions. Group scores on questionnaires and behavioral tests (MIQ-3,

Corsi Block Test, SSS and Wisconsin) were compared using either one-way or repeated measures ANOVA. We used Statistica work-package (Statsoft Inc., Tulsa, OK, USA) for data analysis. Through this paper, the results are presented as mean (±standard deviation – SD), and threshold for significance was set at $P < .05$. Effect sizes were analyzed using partial eta squared (η_p^2).

3. Results

3.1. Questionnaires and executive function assessments

First, no group difference emerged from the comparison of the Corsi block test scores ($F_{(4,66)} = 2.27$, $P = .07$, $\eta_p^2 = .12$), hence showing that all subjects had similar visuo-spatial working memory capacities. Likewise, there was no significant difference between groups when examining mental flexibility with the Wisconsin test, i.e., perseveration ($F_{(4,66)} = .17$, $P = .94$, $\eta_p^2 = .01$), hence suggesting that participants could not have difficulty to integrate "new instructions" in the transfer session. In regard to the individual imagery abilities, we found a significant MI modality effect ($F_{(2,132)} = 10.58$, $P < .0001$, $\eta_p^2 = .13$), but no group ($F_{(4,66)} = .79$, $P = .53$, $\eta_p^2 = .04$) or group × MI modality interaction ($F_{(8,132)} = 1.56$, $P = .14$, $\eta_p^2 = .08$). As expected, Tukey post-hoc revealed that visual scores (internal or external) were systematically higher than kinesthetic scores in all groups ($P < .01$). Therefore, no significant difference was found between MI groups, thus guaranteeing homogeneity in terms of individual ability to elicit motor mental images. The average sleep score, as measured by the PSQI, was 2.30 ± .64, thus attesting to the "good quality" of sleep in all Night groups. On mean SSS ratings in all participants (Day and Night groups), there was no group difference ($F_{(4,66)} = 1.89$, $P = .12$, $\eta_p^2 = .10$), nor session effect ($F_{(1,66)} = .83$, $P = .36$, $\eta_p^2 = .01$), or group × session interaction ($F_{(4,66)} = 1.19$, $P = .32$, $\eta_p^2 = .06$). With respect to sleep quality, the total sleep time was similar in all participants of the Night groups ($F_{(2,42)} = 2.30$, $P = .11$, $\eta_p^2 = .09$), and none of subjects had trouble sleeping. For a summary see Table 1.

3.2. Behavioral data

First, we aimed to determine whether the five groups (MIV Day, MIC Day, no-training, MIV Night, MIC Night) were comparable in terms of performance during the pre-test session (Table 2). A one-way ANOVA on the mean number of errors did not yield an effect of group ($F_{(4,66)} = 1.50$, $P = .21$, $\eta_p^2 = .08$), while a separate one-way ANOVA on the mean sequence duration did ($F_{(4,66)} = 3.21$, $P < .01$, $\eta_p^2 = .16$). Accordingly, further Tukey post-hoc analyses revealed that the MIV Day group was slower than the MIC Night ($P < .01$).

Then, we performed an ANOVArm on the mean number of errors with group as between-subjects factor and session (pre-test, post-test and retention) as within-subjects factor that did not yield a significant main effect of group ($F_{(4,66)} = 1.56$, $P = .19$, $\eta_p^2 = .08$), nor of session ($F_{(2,132)} = 1.15$, $P = .31$, $\eta_p^2 = .02$), or a group × session interaction ($F_{(8,132)} = .79$, $P = .60$, $\eta_p^2 = .04$). A different pattern of results was observed when using mean movement duration as the dependent measure; the ANOVArm revealed a significant main effect of group ($F_{(4,66)} = 4.43$, $P < .01$, $\eta_p^2 = .21$), and a main effect of session ($F_{(2,132)} = 96.69$, $P < .0001$, $\eta_p^2 = .59$), as well as a group × session interaction ($F_{(8,132)} = 3.43$, $P < .001$, $\eta_p^2 = .17$). Accordingly, Tukey post-hoc analyses showed that all groups significantly improved their performance between the pre- and post-test sessions ($P < .05$ for all), while only the MIV Night group further decreased sequential movement duration during the retention session ($P < .001$; Fig. 2). In contrast, subjects from the other groups did not show any significant change in performance between the post- and retention sessions ($P > .05$ for all). These results indicate that only variable training with MI followed by a night of sleep can lead to an additional gain in performance, while the simple passage of time did not ($P = .10$ in the MIV Day). In contrast, subjects from the constant MI groups did not show any additional benefits after a night or a day-time consolidations, but rather stabilized their performance ($P = .10$ for both MIC groups). Finally, the exposure to the two practice sessions (pre- and post-test), in the absence of a specific training was sufficient to yield a performance increase in the no-training group, albeit no further changes has been revealed during the retention session.

In the following analysis, we then focused on the effect of constant and variable MI training (or no-training) on the transfer of performance. We compared the mean number of error during the pre-test with those in the transfer using an ANOVArm. The results showed no main effect of group ($F_{(4,66)} = 1.87$, $P = .12$, $\eta_p^2 = .10$), or session ($F_{(1,66)} = .004$, $P = .94$, $\eta_p^2 < .001$), or group × session interaction ($F_{(4,66)} = .87$, $P = .48$, $\eta_p^2 = .05$). The ANOVArm on the movement duration showed a main effect of group ($F_{(4,66)} = 4.06$, $P < .01$, $\eta_p^2 = .19$), a main effect of session ($F_{(1,66)} = 23.49$, $P < .0001$, $\eta_p^2 = .26$), as well as a significant group × session interaction ($F_{(4,66)} = 3.85$, $P < .01$, $\eta_p^2 = .18$). Accordingly, further Tukey post-hoc analyses revealed that only the MIV Night group improved its performance from the pre-test to the transfer session ($P < .0001$, Fig. 3).

3.3. Assessment of imagery performance

During MI training, the MIC and MIV groups took on average 6.25 ± .45 s and 6.32 ± .49 s respectively to mentally rehearse the sequential motor task. An ANOVArm did not yield a significant group effect ($F_{(3,52)} = 1.50$, $P = .22$, $\eta_p^2 = .07$), or session effect ($F_{(1,52)} = 2.19$, $P = .14$, $\eta_p^2 = .04$), or group × session interaction ($F_{(3,52)} = 1.84$, $P = .15$, $\eta_p^2 = .09$). These data showed no difference between these MI times and the corresponding actual times recorded during the pre-test session, hence demonstrating that the participants complied with the imagery guidelines and therefore preserved the temporal characteristics of the movement during mental rehearsal. There was no group difference when com-

Table 1
Motor imagery characteristics and neuropsychological test scores in the MIV Night, MIC Night, MIV Day, MIC Day and no-training groups. Statistical analysis did not yield any difference between groups in any of these parameters. Results are shown as mean ± SD. *PSQI* Pittsburg Sleep Quality Index, *SSS* Stanford Sleepiness Score, *MIQ*-3 Movement Imagery Questionnaire, *VI* internal visual imagery, *VE* external visual imagery, *K* kinesthetic imagery and Wisconsin (i.e., perseveration).

GROUP	PSQI	SSS		MIQ-3					Corsi	Wisconsin % perseveration
		SSS1	SSS2	VI	VE	K	Total	MI quality		
MIV Day		2.14 (.66)	1.93 (.73)	21.08 (1.14)	21.54 (1.08)	19.38 (1.03)	62.00 (2.77)	3.54 (.51)	5.62 (.96)	19.71 (3.41)
MIC Day		2.15 (.80)	1.85 (.80)	22.38 (1.15)	22.85 (1.30)	18.54 (1.51)	63.77 (53.31)	3.69 (.63)	5.08 (1.19)	20.77 (4.28)
No-training	2.55 (1.04)	2.73 (.47)	2.36 (.67)	22.36 (1.40)	22.82 (1.15)	22.27 (1.45)	67.45 (2.80)		5.73 (.47)	18.33 (5.13)
MIV Night	1.92 (.79)	2.00 (.74)	2.25 (.62)	22.58 (.93)	23.42 (1.33)	20.08 (1.18)	66.08 (2.38)	3.87 (.51)	4.92 (.35)	18.21 (4.61)
MIC Night	2.25 (.89)	2.04 (.58)	2.22 (.65)	19.16 (1.11)	19.31 (1.19)	19.71 (1.55)	66.17 (3.31)	3.63 (.48)	4.08 (.40)	20.19 (6.61)

Table 2
Mean (SD) number of errors and mean movement duration (s) in the MIV Night, MIC Night, MIV Day, MIC Day and no-training groups. All groups increased their performance significantly in the post-test session, while only the MIV Night group further showed a significant improvement during the retention test. Differences between group are indicated with letters, while '*' underlies difference within group.

	Number of errors				Movement duration (s)			
	Pre-test	Post-test	Retention	Transfer	Pre-test	Post-test	Retention	Transfer
MIV Day[a]	0.62 (.18)	0.69 (.20)	1.62 (.47)	1.15 (.33)	7.33 (.43)[e]	6.49 (.39)***	6.27 (.39)	6.93 (.43)
MIC Day[b]	1.38 (.40)	1.00 (.29)	0.77 (.22)	2.08 (.60)	6.83 (.41)	6.20 (.46)*	5.89 (.33)	6.56 (.46)[d]
No-training	1.40 (.44)	1.47 (.43)	1.31 (.81)	0.67 (.28)	6.22 (.33)	5.46 (.24)***	5.62 (.27)	6.14 (.32)[d]
MIV Night[d]	1.40 (.32)	1.6 (.33)	2.30 (.47)	1.50 (.39)	6.24 (.26)	5.33 (.25)***	4.57 (.17)***	5.16 (.23)[b,c,d]
MIC Night[e]	2.33 (.57)	2.00 (.49)	2.00 (.53)	1.87 (.58)	5.83 (.26)[a]	5.02 (.23)***	5.00 (.24)	5.51 (.26)[d]

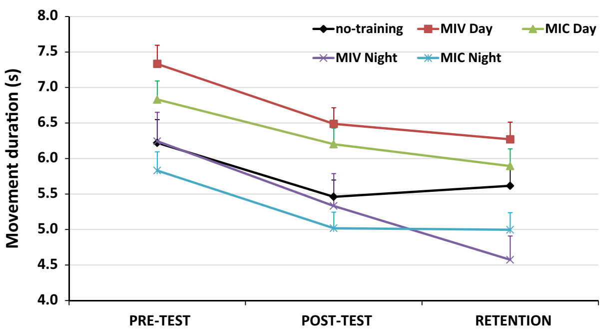

Fig. 2. Mean (SD) movement duration during the 3 experimental sessions. All groups increased their performance significantly in the post-test session, while only the MIV Night group further improved his performance after a night of sleep.

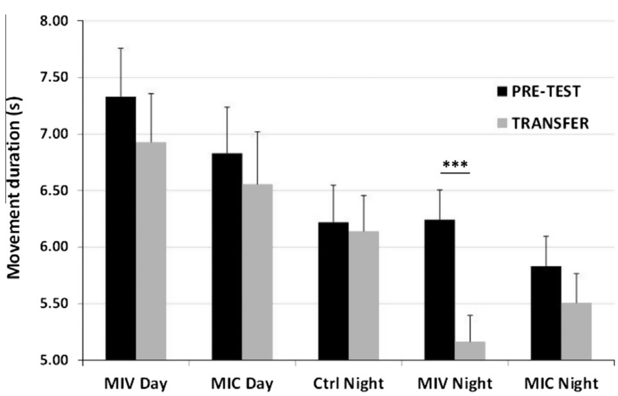

Fig. 3. Beneficial effect of the variable MI practice added with a night of sleep consolidation in transfer of performance. Only the MIV Night group demonstrated significant benefits in the transfer of performance on a new sequential finger task compared to all other groups. These findings suggest that variable MI training followed by a night of sleep might be a relevant condition, rather than constant training or no-training, to enhance the transfer of motor skills.

paring the subjects' ratings in evaluating the vividness of their mental images during MI practice ($F_{(3,52)} = .89$, $P = .45$, $\eta_p^2 = .05$, see Table 1 for mean evaluations per group). Furthermore, during the debriefing following MI, all participants reported that they used the imagery type outlined in the scripts. They combined internal visual and kinaesthetic imagery without switching to external visual imagery. None reported changing the imagery script to suit individual needs, and all rehearsed the motor sequence as requested.

4. Discussion

This study was devised to investigate the effects of constant and variable patterns of training with MI on the acquisition, consolidation and transfer of visuomotor sequential learning. The first aim of the present work was to further investigate the impact of different structural patterns of training (i.e., constant vs. variable) with MI on memory acquisition of a newly learned sequence of movements. We found that both MIC and MIV groups yielded a significant and comparable improvement in performance immediately following MI training. Additionally, we aimed to test whether the nature of consolidation (i.e., Night vs. Day) had different effect on motor performance, with respect to the structure of MI training, and found greater offline delayed gains in performance after a night of sleep for the MIV Night group, whereas those in the other groups stabilized their performance in the retention test. Finally, we aimed to determine which association between the type of MI training and consolidation would provide better transfer in performance to unpractised movement, and found again that the MIV Night group outperformed all the others.

Typically, previous works have shown that constant patterns of overt practice lead to better within-day acquisition compared to variable patterns. Inconsistently, albeit in line with the data by Coelho et al. (2012), we found that both constant and variable MI practices produced an equivalent improvement in performance during the acquisition session (i.e., post-test). Although several findings reported that MI practice improves motor performance in the same way as physical practice, an antagonist growing body of research underlies the differences between these two types of practice (Calmels, Holmes, Lopez, & Naman, 2006; Walsh & Rosenbaum, 2009). Among others, we previously demonstrated that MI practice, rather than physical practice, allowed for a less retroactive interference and flexible representation of the task requirements after a consolidation period that included a night of sleep (Debarnot, Maley, Rossi, & Guillot, 2010). In the same vein, the present results support those by Coelho et al. (2012) who found that variable and constant practices helped learning to the same extent, suggesting therefore that motor representations for acting and for imagining might somewhat be different. However, it is important to note that the no-training group also improved its performance between the pre- and post-tests. It seems likely that this improvement should be due to the Hawthorne effect (i.e., improvements due to practice on the tests themselves, Lied & Kazandjian, 1998), however, this result precludes to draw definitive conclusions on the effect of practice pattern with MI during the acquisition process.

The most salient and novel finding of our study is that variable MI practice resulted in an offline delayed gains in performance after a night of sleep, while a simple passage of time after similar MI practice, as well as constant practice followed by a night or day-time consolidation, did not provide additional benefits but rather stabilized the performance in the retention test. In addition, the no-training group showed a tendency to perform with lower speed in the retention test after a night of sleep. Therefore and in contrast with the observed results during the acquisition process,

these findings provide a partial support of the principle of functional equivalence between MI and physical practice. Indeed, this finding is reminiscent of the data accumulated on the CI effect with physical learning, which have been explained through two main theories: the elaboration hypothesis (Shea & Zimny, 1983, 1988) and the action plan reconstruction hypothesis (Lee & Magill, 1983). Briefly, the elaboration hypothesis suggests that learning skills in a variable manner leads to more elaborative processing, while the reconstruction hypothesis assumes that the learner actively reconstructs several action plans that require more effortful processing. In the end, both hypotheses postulate that the motor skill representation should be more retrievable and permanent in the long term memory. Support for this theory comes from recent neuroimaging studies demonstrating that practice structures that are more cognitively challenging (variable) might rely on the DLPFC for motor-memory consolidation, whereas less cognitively challenging (constant) practice structures might involve the M1 to mediate motor-memory consolidation (Kantak et al., 2010; Lin et al., 2013). So far, there are several data supporting that MI and physical practice share the same neural substrate, although there are also some differences within the pattern of activity in these areas (Hetu et al., 2013). Notably, Lacourse, Turner, Randolph-Orr, Schandler, and Cohen (2004) reported that MI training was accompanied by an increased activation of M1, but to a lesser extent compared to physical practice, while Vry et al. (2012) found that the DLPFC and the parietal cortex are anatomically connected and more activated during MI than actual execution. Based on these findings, we may hypothesize that during constant MI practice, M1 activation might be less important than that of the DLPFC during variable practice, and this "unbalanced-activation" could, therefore, be effective in the motor output following a consolidation period that includes a night of sleep. Using neural modulation approaches, such as rTMS, future works should explored the role of DLPFC and M1 following MI practice, and further determine their role with respect to sleep or day-time consolidation.

Meanwhile, Robertson (2009) stated that the important clues about the consolidation of memories can be afforded from understanding how the brain initially encodes memories. For instance, Robertson, Pascual-Leone, and Press (2004) demonstrated that performance gain was sleep-dependent for explicit procedural learning but time-dependent for implicit skills, hence suggesting that procedural memory consolidation processes may depend on the nature of the task acquisition. These findings are supported by a great number of experimental studies that reported the role of sleep in the offline (re)processing of explicit procedural memory, after a night of sleep, but not after a comparable time interval during daytime (Fischer, Hallschmid, Elsner, & Born, 2002; Karni et al., 1998; Korman et al., 2007; Kuriyama, Stickgold, & Walker, 2004; Song & Cohen, 2014). In the present study, the visuomotor sequences were showed explicitly and subjects (excepted those in the no-training group) were explicitly asked to perform MI, in contrast to when imagined actions are implicit, but not necessarily, engaged (e.g., mental rotation, Jeannerod & Frak, 1999). Therefore, the explicit nature of the MI training may explain why both MIV and MIC Day groups did not improve their performance following day-time consolidation. Moreover, Debarnot, Castellani, and Guillot (2012) reported that the most effective sleep-related performance gains were observed for the most complex imagined movement. Thus, it is possible that the difference in the complexity patterns of MI training (i.e., one sequence during constant training vs. four sequences during variable training) might have differentially impacted the sleep-consolidation processes; with a significant sleep-dependent overnight improvement for the MIV Night group. Overall and as an alternative explanation for the offline gain in performance in the MIV Night group, it is reasonable to assume that the combined effects of the task complexity and the explicit nature of MI training might be more sensitive to the effect of a night of sleep.

Another important finding of the present study is that the MIV Night group showed faster movement speed when executing the new transfer sequence, compared to all other groups. These findings are similar to previous reports that already demonstrated the benefits of variable practice with physical practice in transfer to novel unpracticed task (e.g., Shea, Lai, Wright, Immink, & Black, 2001). Accordingly, Braun, Aertsen, Wolpert, and Mehring (2009) found that when subjects performed variable tasks of the same structure, the motor control process can extract the structure of the task which in turn provide structure-specific facilitation, interference reduction, and exploration. The authors stated that variable training might allow not only to an average mapping, but rather lead to adapt efficiently to related control tasks. Furthermore, Kantak et al. (2011) showed that variable practice might facilitate the transfer of skills especially following a consolidation period that includes a night of sleep, even if they did not directly probe the consolidation processes during sleep. Here we did so and found that variable practice with MI required a night of sleep, rather than a day-time consolidation, to facilitate the abstract knowledge generalization acquired before (i.e., relationship between the goal and actions parameters) and achieve the new sequential movements. However, we acknowledge that it is impossible to definitively rule out that constant and variable MI practice without consolidation might also allow for direct gains in the transfer of performance. Therefore, this hypothesis awaits further experimental investigation to explore the contribution of consolidation in the transfer process following MI practice, with respect to the pattern of structure used during acquisition.

To conclude, our findings confirm that both constant and variable patterns of MI practice provide the same extent of improvement during the acquisition process as already demonstrated by Coelho et al. (2012). Then, we expand these findings to the effect of motor memory consolidation following MI practice by demonstrating that variable practice protracted off-line gains in performance following a night of sleep. Finally, the same pattern of results was found for the transfer of performance with an advantage for the variable MI acquisition after a night of sleep compared to all other experimental conditions. Overall, our findings demonstrate a partial support to the principle of functional equivalence between mental and physical practice as variable MI learning elicits offline gain in performance after a night of sleep whereas constant practice followed either by a night or day-time consolidation did not. A similar conclusion can be drawn about the transfer of performance where variable MI practice associated with a night of sleep might be a potential mean to display highest performance on the skill transfer. Besides theoretic relevance in motor learning, our findings have strong practical applications in (neuro)rehabilitation processes, in which performing MI is cost effective and easily feasible (Butler & Page, 2006; Page, Levine, & Leonard, 2007). The present data contribute to the accumulated evidences that MI and motor performance share common characteristics, and provide new insight in the differences between these two types of practice, during the motor learning processes (i.e., acquisition, consolidation and transfer). Moreover, our findings suggest that practice with variable MI should be preferentially incorporated during the classical course of physical therapy, and it seems to be more valuable before a period of sleep, to benefit from the offline motor consolidation and transfer in unpracticed skills during the recovery process.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.nlm.2014.12.010.

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